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Research article

Climate change and land management impact rangeland condition and sage-grouse habitat in southeastern Oregon

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Abstract: Contemporary pressures on sagebrush steppe from climate change, exotic species, wildfire, and land use change threaten rangeland species such as the greater sage-grouse (*Centrocercus urophasianus*). To effectively manage sagebrush steppe landscapes for long-term goals, managers need information about the potential impacts of climate change, disturbances, and management activities. We integrated information from a dynamic global vegetation model, a sage-grouse habitat climate envelope model, and a state-and-transition simulation model to project broad-scale vegetation dynamics and potential sage-grouse habitat across 23.5 million acres in southeastern Oregon. We evaluated four climate scenarios, including continuing current climate and three scenarios of global climate change, and three management scenarios, including no management, current management and a sage-grouse habitat restoration scenario. All climate change scenarios projected expansion of moist shrub steppe and contraction of dry shrub steppe, but climate scenarios varied widely in the projected extent of xeric shrub steppe, where hot, dry summer conditions are unfavorable for sage-grouse. Wildfire increased by 26% over the century under current climate due to exotic grass encroachment, and by two- to four-fold across all climate change scenarios as extreme fire years became more frequent. Exotic grasses rapidly expanded in all scenarios as large areas of the landscape initially in semi-degraded condition converted to exotic-dominated systems. Due to the combination of exotic grass invasion, juniper encroachment, and climatic unsuitability for sage-grouse, projected sage-grouse habitat declined in the first several decades, but increased in area under the three climate change scenarios later in the century, as moist shrub steppe increased and rangeland condition improved. Management activities in the model were generally unsuccessful in controlling exotic grass invasion but were effective in slowing woodland expansion. Current levels of restoration treatments were insufficient to prevent some juniper expansion, but increased treatment

rates under the restoration scenario maintained juniper near initial levels in priority treatment areas. Our simulations indicate that climate change may have both positive and negative implications for maintaining sage-grouse habitat.

Keywords: climate change; exotic grass; greater sage-grouse; landscape modeling; rangeland management; sagebrush steppe; western juniper; wildfire

1. Introduction

Sagebrush steppe ecosystems are broadly distributed throughout the western U.S., but are also highly imperiled due to a wide range of factors, including species invasions, altered fire regimes, intensive historic livestock grazing, development, and other pressures [1,2,3,4]. The greater sage-grouse (*Centrocercus urophasianus*) is a sagebrush-obligate species that was once widespread but has declined to 56% of its historical distribution in recent decades as quality sagebrush steppe habitat has diminished [5]. Sage-grouse is a challenging species to manage due to its broad distribution, complex life history, and varied habitat requirements for wintering, brood rearing, lekking and other life stages [6,7,8,9]. The greater sage-grouse was considered for listing under the Endangered Species Act in 2010 and was found to be “warranted, but precluded” [10], meaning that the species was recognized as warranting protection based on current threats but would not receive protection due to other species of higher priority. The listing decision will be reconsidered in 2015, and there is a need for scientific information about the likely impacts of invasive species, climate change, disturbances and other threats, and management actions that may be required for long-term maintenance of sage-grouse habitat.

Species invasions have dramatically changed the shrub steppe landscape over the last century, creating novel community types and altering the distribution and extent of native communities across the landscape [11,12,13]. One of the primary causes of change is the introduction of exotic annual grasses, including cheatgrass (*Bromus tectorum* L.), medusahead (*Taeniatherum caput-medusae* (L.) Nevski), and others. These exotic grasses are winter annuals that complete their life cycle earlier in the spring than native perennial bunchgrasses, taking advantage of abundant winter and spring moisture. They tend to be highly competitive in warm, dry environments, particularly following disturbance, and senesce to form a dense layer of dry fine fuels later in the summer that can substantially shorten the fire return interval [14,15]. Another contemporary threat to shrub steppe ecosystems comes from expansion of western juniper (*Juniperus occidentalis* Hook.) beyond its historic range. Western juniper is native to eastern Oregon but has expanded rapidly over the past 140 years into cool, moist sagebrush steppe and other sites near seed sources, converting it to woodlands [12,16]. Juniper expansion has resulted from a variety of factors, including fewer fires due to fire suppression and intensive livestock grazing, increasing precipitation in recent decades, and other factors [3,17]. Juniper expansion into shrub steppe can result in loss of habitat for sagebrush-obligate wildlife species such as sage-grouse, increased soil erosion, and reduced forage production [3,13,18].

Maintaining sage-grouse habitat into the future may prove to be increasingly difficult as climatic changes affect rangeland vegetation. The region has seen large wildfires in recent years, including the Long Draw, Holloway, and Miller Homestead fires, which burned over 1.6 million

acres of Oregon rangelands in 2012. With increasing temperatures, drier summers and reduced snowpack projected for the Pacific Northwest, climate change will likely lead to even more wildfire in coming decades [19,20,21]. Climate change will also likely shift vegetation communities and may create opportunities for restoration in areas with currently degraded condition [22], and may exacerbate the effects of other stressors [23,24]. Although the uncertainty posed by many differing climate models adds to the uncertainty in land management planning, to effectively manage for long-term goals, managers will need to consider the potential impacts of climate change. Information on patterns and effects of climate change may be used for planning the types and locations of sagebrush steppe restoration efforts, allowing managers to prioritize treatments in areas where they are most likely to be effective in restoring high quality sage-grouse habitat into the future.

Restoration of sagebrush steppe has proven difficult, given the vast expanses of shrub steppe in need of restoration, difficulty in establishing native plants, and expense of treating large areas [25]. Much of the sagebrush steppe is located on public lands, and federal agencies generally have insufficient budgets available for restoration, particularly in recent years as an increasingly large proportion has been allocated to fire suppression (e.g., USDA Press Release No. 0184.14). Restoration activities commonly practiced in sagebrush steppe include juniper cutting, prescribed burning, sagebrush thinning, and post-fire stabilization. Effective methods for reducing encroaching juniper woodlands have been established [3], but juniper is rapidly expanding in many areas, and it is usually not possible to locate and treat all encroaching trees. In contrast, it can be very difficult to restore native communities invaded by exotic grasses in warm, dry environments due to the complex and often unpredictable interaction of site potential, wildfire, climate, invasive species, and management practices [25]. In addition, the challenges of combating species invasions and other challenges in rangeland management are broad-scale issues crossing large, interconnected landscapes that are difficult to effectively manage in isolation. For example, exotic grass encroachment on one land holding or allotment can lead to accumulation of fine fuels that can trigger large, severe wildfires across administrative boundaries, fostering invasion over increasingly larger landscapes. To help address these challenges, land managers need tools to assess the long-term effectiveness of management strategies for restoring sage-grouse habitat across large, diverse landscapes.

In this study, we simulated varying scenarios of climate change and land management using a linked dynamic global vegetation model (DGVM), climate envelope model (CEM), and state-and-transition simulation model (STSM) approach. We evaluated combinations of four climate scenarios and three management scenarios, and reported the impacts on projected rangeland condition and sage-grouse habitat across a 23.5 million acre, multi-owner landscape in eastern Oregon. Our results can be used to compare outcomes among scenarios and evaluate potential patterns that may emerge from the intersection of climate change and land management.

2. Materials and Methods

2.1. Study area

The study area is a 23.5 million acre area in southeastern Oregon, covering the entire current range of sage-grouse in the state. Of this area, 20 million acres were modeled, with the remainder of the landscape in agriculture, urban, or non-modeled vegetation types. We divided the landscape into potential vegetation types (PVTs), which represent the biophysical environment based on the

dominant vegetation, soils and other environmental factors. PVT maps were from the Integrated Landscape Assessment Project (ILAP), and are available on the Western Landscapes Explorer website (<http://westernlandscapesexplorer.info>). The study area mostly consisted of shrub steppe PVTs, with the predominant distinction between dry and moist shrub steppe. Dry shrub steppe occupied 47% of the landscape and is characterized by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young) with dry-site grasses such as bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) Á. Löve), and some pockets of saltbush (*Atriplex* spp.). Moist shrub steppe (22% of the initial landscape) is primarily dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle) and bitterbrush (*Purshia tridentata* (Pursh) DC.) shrub species with moist-site grasses such as Idaho fescue (*Festuca idahoensis* Elmer). Within the shrub steppe, we also delineated xeric shrub steppe (15% of initial landscape), where vegetation composition is similar to other shrub steppe, but hot and dry summer conditions make it climatically unsuitable for sage-grouse (see below). We omitted lowland salt desert shrub communities surrounding playas (characterized by greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.) and saltgrass (*Distichlis spicata* (L.) Greene)) from our analysis, as they are restricted to topographic features that are not adequately modeled using our method. At upper elevations, forested communities were divided into dry and moist forest types. Dry forest types occupied 15% of the initial landscape and primarily consisted of Ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), lodgepole pine (*Pinus contorta* Douglas ex Loudon), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.). Moist forest types (2% of the initial landscape) were characterized by Douglas-fir, white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.).

2.2. Modeling process

2.2.1. Modeling overview

Models provide an integral tool for managing under the uncertain future posed by climate change, and simulation modeling provides a framework to project future vegetation condition and make comparisons among alternative scenarios. In this study, we combined three models to evaluate the impacts of climate change and management on rangeland condition and potential habitat for sage-grouse, including a DGVM, a CEM, and a STSM (Figure 1). DGVMs are process-based ecosystem models that simulate changes in plant functional types, carbon stocks, and other ecosystem properties. Although they can simulate the effects of climate change on broad vegetation communities, DGVMs do not incorporate more detailed community dynamics, such as invasion by exotic species, or incorporate management activities. CEMs characterize the relationship between locations of known species presence and mapped climate variables, but do not account for biotic effects, such as competition or vegetation structure, that also shape species distributions. STSMs provide a simple and flexible tool for simulating vegetation dynamics and projecting the effects of management on vegetation composition and structure. STSMs have been used widely in planning efforts for landscape assessments and management plans, but their utility for longer-term planning is limited because they do not directly incorporate the effects of climate change. Here we combine the three approaches, resulting in climate-informed STSMs (cSTSMs) that can be used to evaluate

possible changes in potential vegetation, fire regimes, vegetation composition, and wildlife habitat under multiple scenarios of climate and management. Each model is described in the following paragraphs in more detail. Similar studies linking DGVMs and STSMs have been completed in the recent past for rangeland [26] and forested environments [27,28], but this study is unique in its incorporation of a CEM. Our work therefore integrates many components, including succession, disturbance, climate, management and habitat. It is intended to identify major trends in indicators of rangeland condition and compare alternative future scenarios across broad spatial scales and over long time frames.

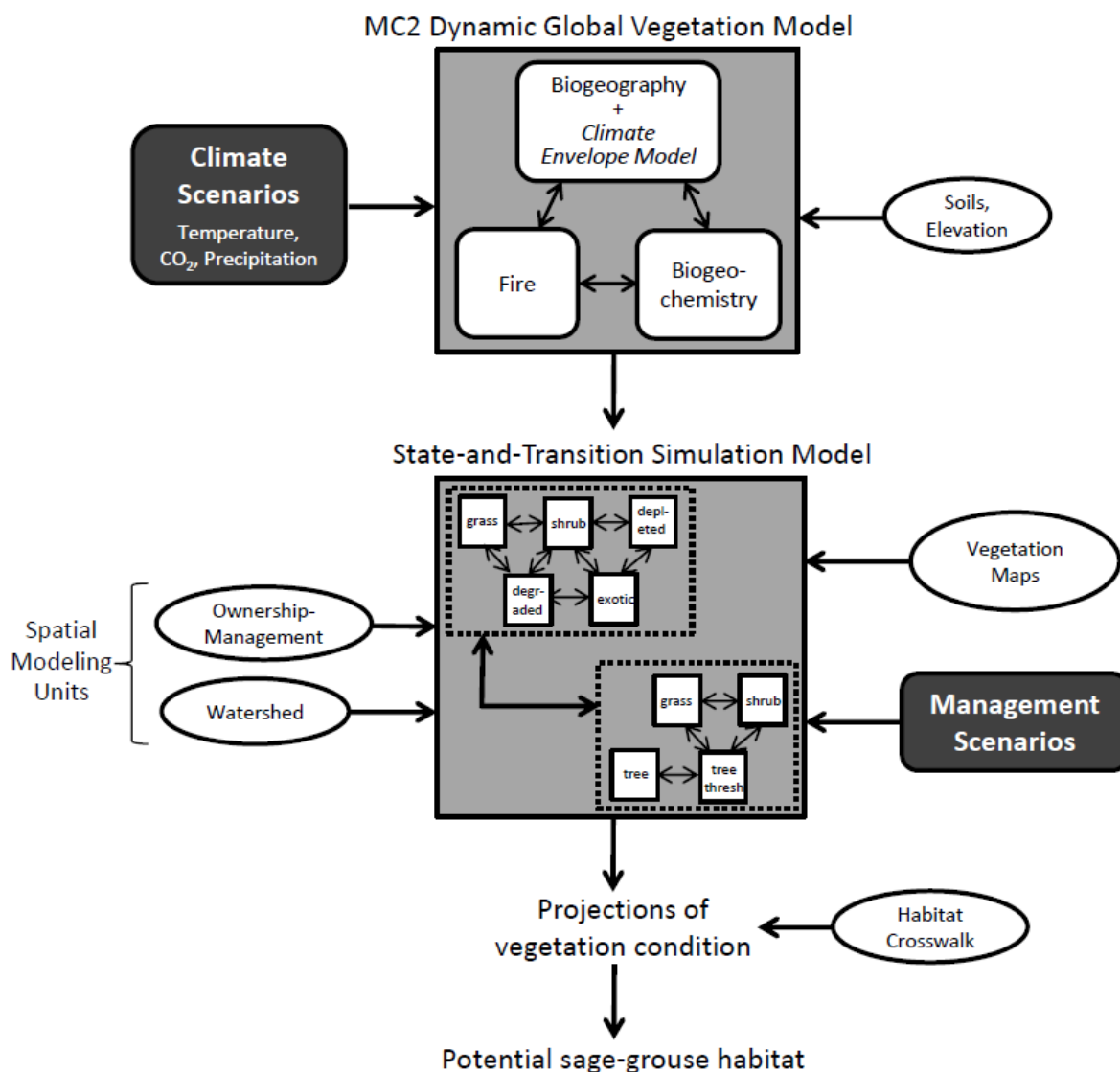


Figure 1. Conceptual diagram of model linkages and inputs. Climate projections from multiple climate scenarios were input into the MC2 dynamic global vegetation model. MC2 consists of three modules (biogeography, fire, and biogeochemistry), and a habitat-climate ruleset was added to the biogeography module based on a climate envelope model. Change in the extent of plant functional types and trends in wildfire from MC2 were incorporated into a climate-informed state-and-transition simulation

model (cSTSM), which consists of linked STSMs, each shown as a simplified example in dashed boxes. The cSTSM was run across 806 modeling units under multiple management scenarios to project rangeland vegetation condition and potential future sage-grouse habitat under varying assumptions about climate and management.

2.2.2. MC2 dynamic global vegetation model

MC2 is a DGVM that simulates change in plant functional types, carbon stocks, nutrient flows, and other ecosystem properties, and is composed of three interacting modules that simulate biogeography, biogeochemistry, and wildfire. MC2 is the product of rewriting the original MC1 DGVM [29] to run faster and use less disk space, and is freely available online (<https://sites.google.com/site/mc1dgvusers/home/mc2>). In this study we used MC2 version 2B105, which incorporates modifications to the biogeography and fire modules. The biogeography module simulates changes in the distribution of broad plant functional types (e.g., temperate needleleaf woodland, temperate grassland). It uses a series of biogeographical rulesets that were originally based on the MAPSS model [30], but have since been extensively revised, as documented in the Supplementary MC2 Biogeography Model Description. The biogeochemistry module is a modified version of the CENTURY model [31] and simulates plant growth, organic matter decomposition, and the movement of water and nutrients through the ecosystem. The MC2 fire module simulates the initiation, behavior, and effects of fire based on fine fuel moisture and fuel buildup [32]. Inputs to MC2 include soil properties, elevation, latitude, and climatic conditions (precipitation, monthly means of diurnal extreme temperatures, atmospheric water content, and atmospheric CO₂). MC2 was calibrated regionally to match the MC2 simulated historic vegetation distribution with PVT maps. We also calibrated fire parameters to simulate expected historic fire rotations based on LANDFIRE data (www.landfire.gov), which were later adjusted to reflect current levels of fire (see Model integration). The MC2 biogeography rule set used in this study differed from previous similar studies [26,33] by incorporating improvements in the modeling of rangeland ecosystems, detailed in the Supplementary MC2 Biogeography Model Description.

To estimate the effects of climatic conditions on potential sage-grouse habitat, we developed a simple ruleset to describe a climatic zone where sage-grouse are absent in our landscape with a classification tree model. This rule set differentiated the two major types of shrub steppe (moist and dry, where conditions are climatically suitable for sage-grouse), from xeric shrub steppe, where conditions are climatically unsuitable for sage-grouse. Sage-grouse presence in southeastern Oregon is shaped by the interaction of vegetation and climate, and variables describing conditions of summer drought appear to be the most effective variables for delineating areas where sage-grouse are absent in the region (Henderson et al., manuscript in preparation). Although climatic constraints to sage-grouse distributions are more complex than just summer moisture stress, our modeling approach demands a simple rule set to delineate vegetation types and habitat constraints.

We built the classification tree model from data points of known sage-grouse locations (telemetry data and lek locations) and a regular grid of background ‘absence’ points. These points were related to a suite of historic climate summaries, averaged over the last 30 years, derived from the PRISM dataset (PRISM Climate Group, Oregon State University) with a binary classification tree model [34]. We selected the terminal node of the classification tree model that contained the fewest sage-grouse presence points, and identified the variables and thresholds leading to that node

to develop a ruleset describing climatic conditions that were negatively correlated with sage-grouse. The first variable/threshold described low summer (June, July and August) precipitation (< 4.7 cm), and the second described high maximum August temperatures (> 29.5 °C), and the third described high annual average temperatures (> 8.7 °C). When applied to the modeling dataset, these three rules identified a set of points that comprised 96% background points and 4% sage-grouse presence points, while the remaining set of points contained 60% background and 40% presence points. The data used to build the climate envelope model was based on 30-year average values, whereas the threshold defined in the MC2 biogeography module was based on temporally smoothed estimates of temperature and precipitation (exponential smoothing with $\tau = 10$ years). Because of the differences in timeframe of summary between the CEM and MC2, and the subsequent over-prediction of xeric shrub steppe in our initial maps, we adopted a lower summer precipitation threshold (< 3.8 cm summer rainfall). This yielded a conservative estimate of the capacity for summer drought to constrain sage-grouse, which we deemed most appropriate for our application. Ultimately, areas occupied by shrub steppe vegetation that met these criteria were classified as xeric shrub steppe.

2.2.3. State-and-transition simulation models

State-and-transition models (STMs) provide a conceptual framework for describing ecological dynamics and evaluating assumptions about vegetation change [35,36,37,38]. STMs that have been parameterized with transition probabilities and used to generate future projections have more recently been termed STSMs (state-and-transition *simulation* models), and can be used to evaluate alternative management actions and explore a variety of management options [39,40,41,42]. STSMs can be thought of as box and arrow models, where boxes represent vegetation communities defined by their composition and structure. Transitions link boxes together and represent processes such as succession, natural disturbances (e.g., wildfire and insect outbreaks), and management activities (e.g., livestock grazing, juniper removal, or prescribed fire).

Each STSM is used to describe the vegetation dynamics (e.g., succession rates, fire rotation, invasion probability, etc) that are characteristic of a PVT. The shrub steppe STSMs in this study are described in detail in Creutzburg et al. [26], and are only briefly summarized here. Major state classes in the dry shrub steppe PVT include native shrub steppe, semi-degraded shrub steppe (partial dominance of native and exotic grasses), exotic shrub steppe, depleted shrub (high shrub cover and low herbaceous cover), and seeded non-native shrub steppe (e.g., crested wheatgrass (*Agropyron cristatum* (L.) Gaertn.)). In the moist shrub steppe PVT, the major state classes are native shrub steppe, semi-degraded shrub steppe (containing ruderal grasses that are tolerant of disturbance), exotic shrub steppe, and juniper woodlands. Juniper woodlands are divided into three phases, with phase I representing shrub steppe with scattered juniper, phase II with codominant juniper and shrubs/grasses, and phase III indicating juniper-dominated woodlands [3]. A list of shrub steppe state classes with descriptions is provided in Supplementary Table S5. The major transitions in the STSMs include succession, wildfire, livestock grazing, drought, insect outbreaks, natural regeneration of native herbs, juniper seeding, and management activities. Wildfire probabilities vary among STSMs and with the level of exotic grass dominance within individual STSMs based on an analysis of the Monitoring Trends in Burn Severity (MTBS) dataset across the study region [26,43]. Annual transition multipliers describe variability in wildfire, drought, and insect outbreaks from year to year.

Forested STSMs were from the Integrated Landscape Assessment Project (<http://westernlandscapesexplorer.info/IntegratedLandscapeAssessmentProject>) but occupy a small proportion (17%) of the landscape and do not provide sage-grouse habitat; therefore they are not a focus of this analysis.

2.2.4. Model integration

To integrate information from MC2 into the STSMs, we combined the individual STSMs representing each PVT into one interconnected cSTSM (Figure 1). A description of the model integration is provided in Halofsky et al. [33], and here we briefly summarize the process and note where our approach differed from previous studies. We incorporated two major types of information from MC2 into the STSMs: changes in PVT extent, and wildfire trends. To simulate changes in PVT extent, transitions among PVTs were added to allow shifts in vegetation types based on climate-related vegetation shifts in MC2. Under our current climate scenario, we deactivated these inter-PVT transitions. Under the three climate change scenarios, we extracted annual PVT to PVT transition probabilities from MC2 output within the R environment for statistical computing (package: MC2toPath). For each climate change scenario, PVT transition rates were calculated for each time step by tallying the number of pixels within each PVT that transitioned to another PVT at the next time step. The tally was translated to a probability by normalizing by the area (number of pixels) of the initial PVT within the first timestep. The average values of all of these time-series were used to set transition probabilities describing PVT to PVT transitions within the cSTSMs. The time series was then translated into a multiplier file, which functions in the STSMs to modify the probability of each transition up (value > 1) or down (value < 1), simulating interannual variability. The inter-PVT multipliers for each PVT pair were calculated as the fraction of the area occupied by the first PVT that transitioned to the second in a given time-step. The time-sequence for these transitions was normalized to 1 by dividing each value by the average transition probability for the whole sequence.

Within the cSTSMs there are two types of inter-PVT transitions: climate-related shifts in vegetation types, and climate-related shifts in habitat suitability. Inter-PVT vegetation transitions are limited to early-successional state classes, under the premise that stand-replacing disturbances will often be the catalyst for change in site potential [44]. Therefore, a major disturbance is required for an inter-PVT vegetation transition to occur. In contrast, inter-PVT *habitat* transitions (to or from xeric shrub steppe) are allowed to occur any year from any state class in the model. Therefore, habitat transitions reflect inter-annual variability in temperature and precipitation that can drive rapid shifts to and from the xeric shrub steppe vegetation type, even in the absence of disturbance.

We also incorporated information about changing wildfire frequencies from MC2. We extracted the fraction of grid cells burned across all cells in the MC2 simulations and normalized the burned fraction to the wildfire probability in the cSTSMs. Then, we created a multiplier to adjust the annual wildfire probabilities in the cSTSM based on future trends and interannual variation in wildfire. These fire trend multipliers were generated for each PVT by calculating changes in the proportion of cells experiencing fire for each PVT at each time step. This proportion was translated to a multiplier by normalizing to a baseline rate, which we set as the average fire proportion during the first 20 years of our MC2 simulation. Therefore, wildfire projections under climate change reflected both the wildfire probabilities in the original STSMs (based on MTBS data) but were also modified through

time based on annual projected wildfire in the MC2 model.

2.3. *Spatial data*

2.3.1. Modeling units

We stratified the landscape into modeling units, defined by the combination of ownership-management categories and watershed. The ownership-management layer describes land ownership and management intensity (Figure 2). Ownership consisted of BLM lands (69%) (note that US Forest Service lands were a minor part of the landscape and were combined with BLM), private (27%), state (3%), and Fish and Wildlife Service (1%). Management allocation distinguished BLM districts (Vale, Prineville, Burns and Lakeview) and delineated core and low-density sage-grouse habitat maps from the Oregon Department of Fish and Wildlife (downloaded from: <http://www.dfw.state.or.us/wildlife/sagegrouse/>). In the cSTSMs, management treatments were only applied within these sage-grouse habitat areas, and will be called priority treatment areas for the remainder of the paper. Priority treatment areas occupied 50% of the landscape. Watershed was defined as 5th-field (10 digit) Hydrologic Unit Codes (HUCs), a standard federal hydrologic nomenclature [45]. Although individual watersheds were not managed differently or expected to vary in vegetation characteristics, using watershed boundaries allowed summarization of model results at the watershed level. There were 806 modeling units in the study area, and each modeling unit was run as an individual non-spatial simulation.

2.3.2. Initial conditions

Within each modeling unit (ownership-management/watershed combinations), we used two types of vegetation maps to characterize vegetation at the initiation of the simulations, including a PVT map and a current vegetation map. These maps were generated using nearest neighbor imputation, relating environmental variables and (in the case of current vegetation) satellite imagery to vegetation survey plot data [46]. The PVT map describes vegetation potential as defined by climate, soils, dominant species, and disturbance regime, a similar concept to the biophysical setting of the LANDFIRE project or ecological sites of the Natural Resources Conservation Service. The current vegetation map contains detailed information on species composition and percent cover required to assign each pixel to a state class in the STSM. PVT and current vegetation maps are available for download through the Western Landscapes Explorer website (<http://westernlandscapesexplorer.info>). We assigned mapped pixels to state classes through a series of rule sets that related potential vegetation and current vegetation to the model state classes [26].

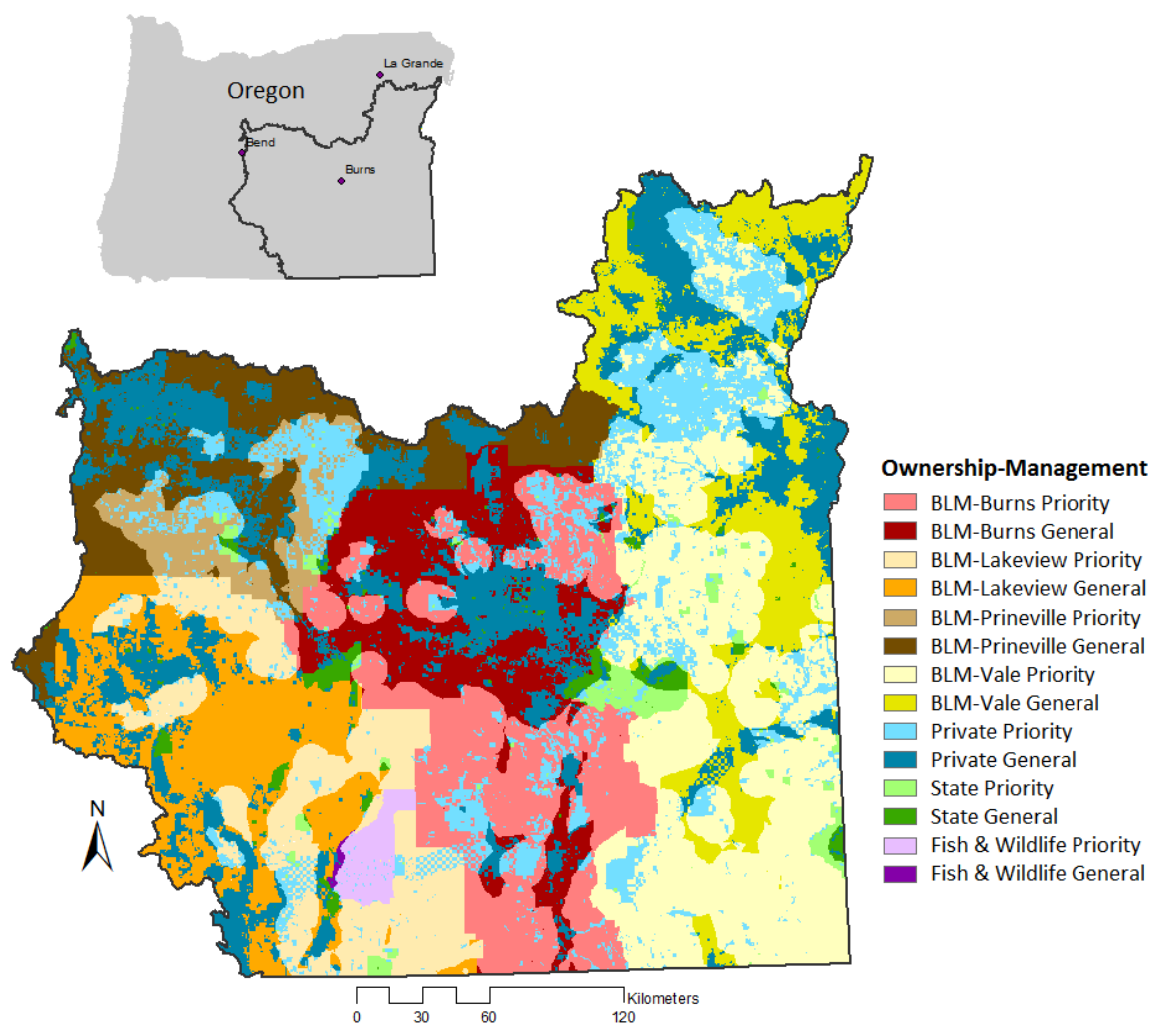


Figure 2. Ownership-management categories in the eastern Oregon study area. Management activities were only modeled only in priority treatment areas (Priority), based on current sage-grouse distribution maps and shown in lighter colors for each ownership type.

2.4. Climate scenarios

We used climate scenarios from three global circulation models in the Coupled Model Intercomparison Project 5 [47]. All models were run under representative concentration pathway 8.5, representing a continuation of high global greenhouse gas emissions levels. The GCMs we chose bracketed much of the future range of expected future trends, and included HadGEM (hot temperatures with drier summers), MRI (warm temperatures and slightly wetter), and NorESM (hot temperatures and much wetter) (Table 1).

Table 1. Temperature and precipitation under current climate (1951–2000) and projected future climate (2081–2100) for each of the three global circulation models used in this study.

	Current Climate	Future Climate (2081–2100)		
		HadGEM	MRI	NorESM
Temperature (°C)				
Winter	–1.4	4.7	1.2	3.3
Spring	6.2	12.0	9.3	10.7
Summer	17.3	26.4	21.8	23.6
Fall	8.0	14.5	11.7	13.1
Annual	7.6	14.4	11.1	12.7
Precipitation (cm)				
Winter	12.4	12.1	13.9	15.7
Spring	10.0	10.8	11.6	12.0
Summer	5.5	4.0	5.1	8.7
Fall	8.1	9.0	7.5	8.7
Annual	36.1	36.0	38.1	45.1

2.5. Management scenarios

We developed three alternative management scenarios, including no management, current management, and a sage-grouse habitat restoration management scenario (called restoration management hereafter). Each of these scenarios was specifically tailored to each ownership-management group based on data and information provided by land managers in the region. All treatments in all scenarios were allocated solely in priority treatment areas to target restoration toward sage-grouse conservation. All scenarios assumed the continuation of fire suppression and livestock grazing, except in the US Fish and Wildlife Service Hart Mountain National Antelope Refuge (hereafter called Hart Mountain Refuge), where all horse and cattle grazing was removed in the 1990s and all grazing transitions were deactivated. A description of the management treatments used in the models is in Table 2. Management treatments were input into the cSTMs as a target number of acres (Tables 3 and 4) for each combination of PVT and ownership-management category, allocated among watersheds within each PVT/ownership-management category based on the size of the watershed (i.e., larger watersheds contained a larger number of treated acres). The exception was for post-fire restoration treatments, which were input as a proportion of the cells within a target state class following wildfire. By setting this treatment as a proportion, we allowed more post-fire restoration in years with more acres burned.

Table 2. Treatment types modeled in the current management and restoration management scenarios. Each treatment is assigned a letter (A–L), corresponding to target treatment rates in Tables 3–4.

Vegetation Type	Management Treatment	State Class Treated	Description
Dry shrub steppe	A Post-fire herbicide & seeding	Exotic grass	Post-fire herbicide and seeding of native species, within 2 years of wildfire. 50% remains in exotic grass.
Dry shrub steppe	B Post-fire seeding	Exotic grass	Post-fire seeding of native species, within 2 years of wildfire. 80% remains in exotic grass.
Dry shrub steppe	C Mechanical thinning	Depleted shrub	Thinning of dense shrub to open shrub with semi-degraded herbaceous condition.
Dry shrub steppe	D Herbicide/ seeding	Semi-degraded	Herbicide and seeding of native species into semi-degraded shrub steppe. 20% remains in semi-degraded condition.
Dry shrub steppe	E Native restoration	Seeded non-native grass	Restoration of seeded non-native plantations by seeding native species. 40% remains in seeded non-native condition.
Moist shrub steppe	F Prescribed fire	Closed shrub	Prescribed fire to thin closed shrub. 80% transitions to open shrub, 20% remains in closed shrub.
Moist shrub steppe	G Mechanical thinning	Closed shrub	Mechanical thinning of closed shrub to open shrub.
Moist shrub steppe	H Prescribed fire	Phase I juniper	Prescribed fire to thin juniper in phase I. 80% returns to herbaceous state, 20% remains in phase I woodland.
Moist shrub steppe	I Prescribed fire	Phase II juniper	Prescribed fire to thin juniper in phase II. 80% returns to herbaceous state, 20% remains in phase II woodland.
Moist shrub steppe	J Juniper cutting	Phase I juniper	Cutting of juniper in phase I. Returns woodlands to closed shrub.
Moist shrub steppe	K Juniper cutting	Phase II juniper	Cutting of juniper in phase II. Returns woodlands to closed shrub.
Moist shrub steppe	L Juniper cutting	Phase III juniper	Cutting of juniper in phase III. Returns woodlands to open shrub.

Table 3. Targeted number of acres in each ownership-management type and management treatment (codes from Table 2) under the current management scenario. Numbers are in acres except for the columns noted with an asterisk (*), indicating values input as a proportion. Note that treatments are only assigned in priority treatment areas, which encompass 50% of the landscape.

Ownership	Management Treatment Code											
	A*	B*	C	D	E	F	G	H	I	J	K	L
BLM-Burns	0.074	0.14	525	787			525	5974	1493	4367	1092	
BLM-Lakeview	0.074	0.14	161				161	431	108	2973	743	
BLM-Prineville	0.074	0.14	141				141	4991	1248	1307	436	436
BLM-Vale	0.074	0.14	585	1849			585	306	76	2555	639	
Other										252	63	
Private										30696	7674	

State	200				400				100			
Total	1412	2836	0	0	1412	11702	2925	42551	10747	436		

Table 4. Targeted number of acres in each ownership type and management treatment (codes from Table 2) under the restoration management scenario. Numbers are in acres except for the columns noted with an asterisk (*), indicating a proportion. Note that treatments are only assigned in priority treatment areas, which encompass 50% of the landscape.

Ownership	Management Treatment Code											
	A*	B*	C	D	E	F	G	H	I	J	K	L
BLM-Burns	0.25		1050	1574	300	525	525	11633	5687	5687	2844	
BLM-Lakeview	0.25		322		150	161	161	3830	1872	1872	936	
BLM-Prineville	0.25		281			141	141	5556	2694	2862	1515	4209
BLM-Vale	0.25		1170	3698	300	585	585	3218	1573	1573	787	
Other										504	126	
Private								15348	3837	15348	3837	
State				400				400	100	400	100	
Total			2823	5672	750	1412	1412	39985	15764	28247	10145	4209

2.5.1. No management scenario

The no management scenario assumed that no management treatments occurred on the landscape. The only difference among ownership-management groups was the exclusion of livestock grazing on the Hart Mountain Refuge.

2.5.2. Current management scenario

The current management scenario was developed in consultation with managers at the BLM Oregon state office, Oregon Department of State Lands, Oregon Department of Fish and Wildlife, Natural Resources Conservation Service, Oregon Watershed Enhancement Board, and the Hart Mountain Refuge (Table 3). Treatments were specified for each land ownership and management allocation across the landscape.

For BLM lands, we used the National Fire Plan Operations and Reporting System (NFPORS) database to obtain acres treated for juniper and shrub treatments, and the Emergency Stabilization and Rehabilitation (ES&R) database for post-fire rehabilitation treatments. In the NFPORS database, we filtered the database based on spatial coordinates to select treatments within the study area from 2005–2012, the years of reliable recorded data. Some treatments were entered multiple times in the database, particularly in the case of multiyear treatments, and therefore we could not simply sum all treated acres within the database. Instead, we created a unique treatment identifier based on the project identification number and the spatial location, and assumed that the maximum number of acres for each treatment identifier was the total number of acres treated. For each BLM district, the number of acres was summed for each of three treatment groups, including mechanical juniper treatment, prescribed fire juniper treatment (broadcast burning only), and sagebrush thinning. We then summed across all treatments and divided by the number of years in the record (8) to obtain an average annual number of acres treated. No information was included about the phase of juniper treated, so we

consulted with BLM experts to approximate the proportion of juniper treatments in phases I, II and III for each BLM district. From the ES&R database, we obtained the acres treated for seeding and weed treatments for a subset of the fires burned in the region from 2005–2013. We divided the number of acres treated by the number of acres of each fire perimeter and determined that an average of 21% of each fire perimeter was treated, with 65% of those treatments as seeding only and 35% as seeding with herbicide.

Current management activities for state lands and the Hart Mountain Refuge were provided through personal communication with managers. Current management treatments for private lands were compiled from data sets provided by the Natural Resources Conservation Service, Oregon Watershed Enhancement Board, and BLM.

2.5.3. Restoration management scenario

The restoration management scenario used the current management scenario as a baseline and was modified to reflect discussions with managers about potential changes to current management practices under a hypothetical increased budget (Table 4). As with the current management scenario, the restoration management scenario treatments were specified for each ownership-management allocation, and were applied only in priority treatment areas. Some managers expressed an interest in using more prescribed fire to control juniper encroachment, as the cost per acre is lower than for cutting. We also modeled treatments that are currently not widely used, such as restoration of seeded crested wheatgrass plantations and prescribed fire to thin sagebrush. In most cases, treatment targets were roughly doubled over current levels, with some changes to the types of treatments. However, the total area treated on private lands in the restoration scenario is identical to the current management scenario. Juniper treatment levels on private lands are currently very high (~ 38,000 acres per year) due to efforts by the Sage Grouse Initiative (www.sagegrouseinitiative.com) and other restoration efforts to address declining sage-grouse habitat, and we assumed increasing these treatment rates above current levels was probably not realistic. The restoration management scenario should not be interpreted as planned actions by any agency, but rather as one possible alternative to compare with current management.

2.6. Running models

cSTSMs were run in the Path landscape model 3.0.4 (<http://www.apexrms.com/>) for 94 years (2007–2100) and five replicate Monte Carlo simulations. Similar previous efforts have run a greater number of Monte Carlo simulations, but due to the large size of the study area and resulting large volumes of simulation output, we limited the number of replicates. Additionally, sensitivity testing indicated that the number of replicates has a minor influence on vegetation dynamics and projected future conditions. The Path model is a non-spatial model; it does not simulate spread of processes between adjacent cells. However, we stratified the landscape spatially using modeling units of ownership-management and watershed, and initialized our models with potential and current vegetation maps (see Spatial Data, above). Therefore, our modeling was semi-spatial. Simulations were run individually for each modeling unit and output could be interpreted as summaries within each modeling unit or could be aggregated to the broader landscape. In this paper, output was aggregated across the landscape and summarized by potential vegetation types and groups of state classes.

2.7. Sage-grouse habitat interpretation

We characterized each of our STSM state classes into three designations: general sage-grouse habitat, high-quality habitat, and non-habitat (Supplementary Table S5). To make these assignments, we used a two-phased approach. For the first phase, we used a dataset that combined a regular grid of 8272 background points and 4713 sage-grouse presence points (telemetry and known lek locations) to rank our state classes according to their correspondence with known sage-grouse locations in the landscape. We intersected the point dataset with our current vegetation map of state classes (see Initial Conditions, above). We then scored each state class according to the percentage of positive vs. background points that intersected it ($> 36\%$ for all habitat, and $> 45.2\%$ for high-quality habitat). Because this method of ranking state classes produced unrealistic results for some of the uncommon state classes due to random sampling error, we modified the assignment for those state classes that occupied $< 1\%$ of the landscape, in cases where literature or expert judgment indicated that the class was likely unsuitable for sage-grouse. This resulted in removing seeded shrub steppe from the high-quality category and phase II juniper woodlands from the general habitat category. Using this method, we designated high-quality habitat as all herbaceous and shrub steppe state classes with a predominantly native grass layer within the moist and dry shrub steppe PVTs. High-quality habitat also included semi-degraded state classes with $< 25\%$ shrub cover in the moist shrub steppe PVT. General habitat included all of the high-quality habitat state classes, plus several others: semi-degraded shrub steppe with $> 25\%$ shrub cover in the moist shrub steppe PVT, seeded shrub steppe with 5–15% shrub cover in the dry shrub steppe PVT, semi-degraded shrub steppe with $< 5\%$ shrub cover in the dry shrub steppe PVT, semi-degraded shrub steppe with $> 15\%$ shrub cover in the dry shrub steppe PVT, and phase I juniper. All state classes in forested models, phase II and III woodlands, state classes with a predominantly exotic grass herbaceous layer, depleted (dense) shrub, and other state classes dominated by seeded grasses were considered non-habitat. A full list of state classes, descriptions, and habitat designation is provided in Supplementary Table S5.

3. Results

3.1. Climate scenarios

3.1.1. Potential vegetation types

Under continuing current climate, PVTs remain unchanged over time, with 47% of the landscape in dry shrub steppe, 22% in moist shrub steppe, 15% in xeric shrub steppe, and 17% in forested types (Figure 3). Under all three climate change scenarios, cSTSM projections indicate increases in moist shrub steppe and declining dry shrub steppe by the end of the century. The MRI climate scenario showed the lowest amount of change and the lowest interannual fluctuations, whereas the HadGEM climate scenario projected high interannual variability and sharper declines in dry shrub steppe. The NorESM scenario projected even greater declines in dry shrub steppe as increasing precipitation caused a ~ 3 -fold increase in moist shrub steppe in the last few decades of the century. The lowest agreement among models was in the extent of xeric shrub steppe, characterized by hot, dry summer conditions that are climatically unsuitable for sage-grouse. The extent of xeric shrub steppe fluctuated widely, particularly in the HadGEM and NorESM climate

scenarios, due to interannual variability in summer temperature and precipitation projections. By the end of the century, the extent of xeric shrub steppe declined to nearly zero under NorESM, declined to roughly 4% of the landscape under MRI, and increased to 27% under HadGEM. All climate change scenarios projected relatively minor changes in forested extent, with small declines in dry forests and increases in moist forests.

3.1.2. Wildfire

Wildfire increased over the course of the simulation in all scenarios (Figure 4). Early in the century, the average area burned in wildfires was roughly 200,000 acres across all climate scenarios. Under current climate, wildfire increased by 26% from early to late-century, due to increases in exotic annual grass state classes. Under the climate change scenarios, the area burned doubled under NorESM and increased by 4× under HadGEM and MRI. The most severe fire years occurred under the Hadley and MRI climate scenarios, with projections of over 2 million acres burned in the most severe years, and multiple years with wildfire exceeding 1.5 million acres by late century.

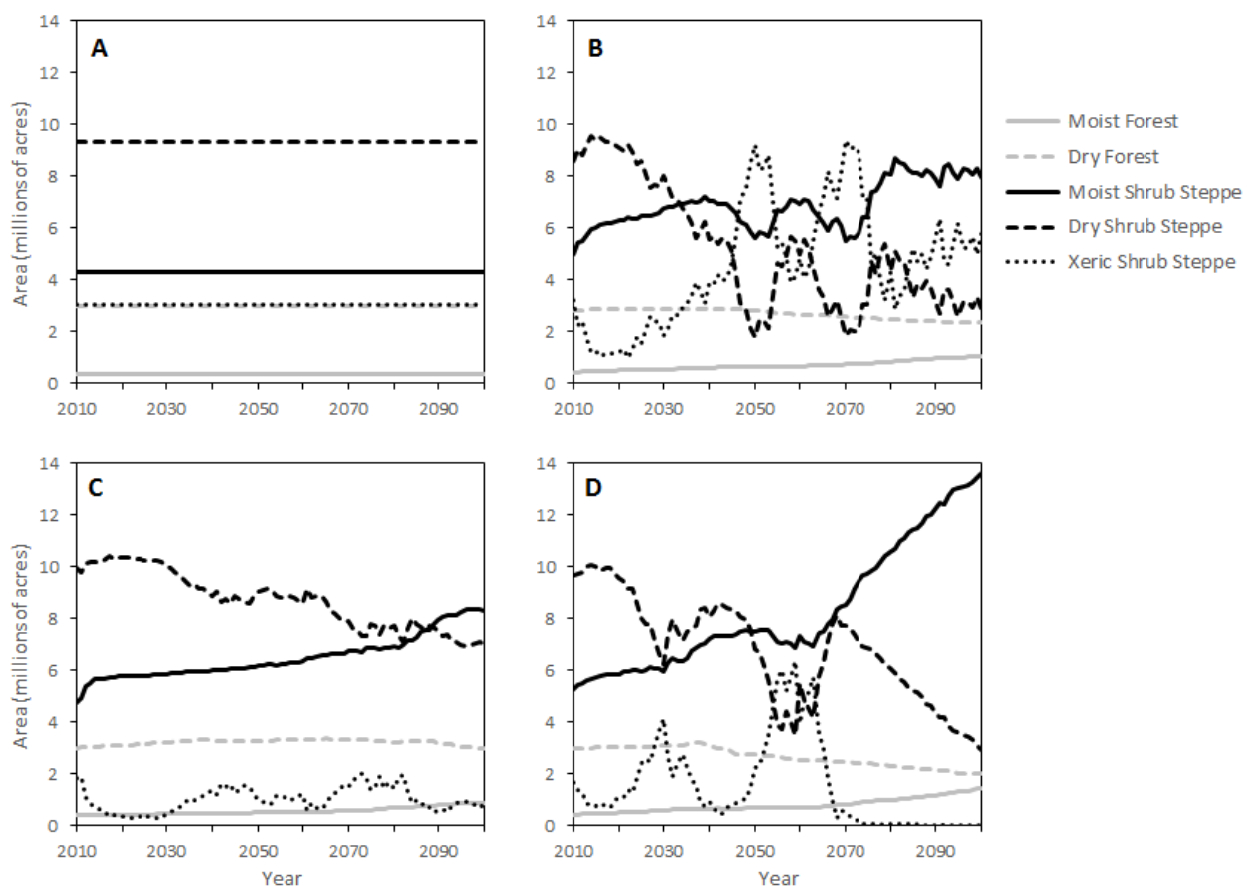


Figure 3. Projected trends in potential vegetation types over time under current climate (A) and three scenarios of climate change, including HadGEM (B), MRI (C), and NorESM (D). Projections are shown without active management (no management scenario).

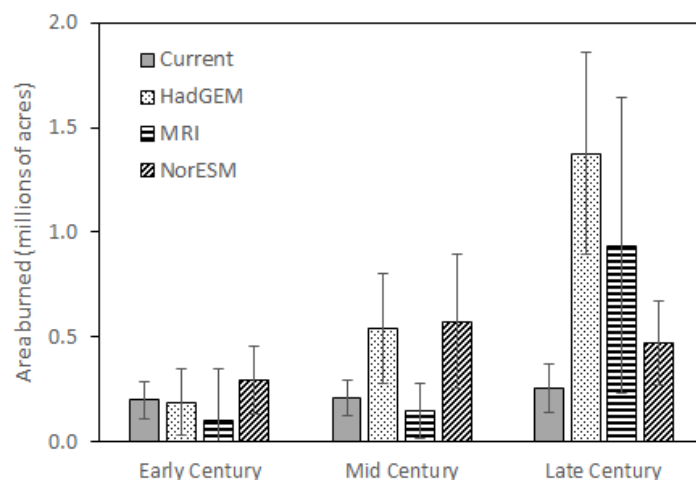


Figure 4. Average annual area burned in wildfires (± 1 SD) in early century (2011–2030), mid-century (2046–2065) and late century (2081–2100) projections. Projections are shown without active management (no management scenario).

3.1.3. Vegetation composition

Vegetation composition (state classes within the cSTSM) across the landscape shifted rapidly under all climate scenarios without active management. The initial landscape was heavily dominated (> 8 million acres) by semi-degraded shrub steppe, which is characterized by partial dominance of the herbaceous layer with exotic species [26]. Under continuing current climate, semi-degraded shrub steppe declined rapidly and was replaced by exotic shrub steppe in the first several decades of the simulations, increasing by $4\times$ initial levels over the century (Figure 5A). Phase I juniper (threshold woodlands) occupied 1.8 million acres at the beginning of the simulations and declined slowly as it converted to woodlands (phases II and III) over the course of the simulation, which expanded from 300,000 acres initially to 4.2 million acres by the end of the century. Overall, juniper encroachment (phases I-III) went from 2.2 million acres at the beginning of the simulations to 4.9 million acres at the end. Native shrub steppe declined to roughly one third of its initial extent, while forested areas and seeded non-native shrub steppe remained relatively stable over time.

Under all three climate change scenarios, exotic grass increased substantially in the first several decades of the simulations but reached lower levels than under current climate (Figure 5B-D). In the HadGEM and NorESM climate change scenarios, exotic grass actually decreased late in the century after initial increases, with NorESM showing a rapid decline in exotic grass during the last three decades back to roughly initial levels. Juniper woodlands increased under all climate change scenarios but reached lower levels than under current climate. Threshold juniper woodlands showed similar patterns to current climate, but juniper woodlands increased to 2 million–3.1 million acres, a lower end-of-century level than projections under current climate. Native shrub steppe increased under all climate change scenarios by the end of the century, with the greatest increases in the NorESM model.

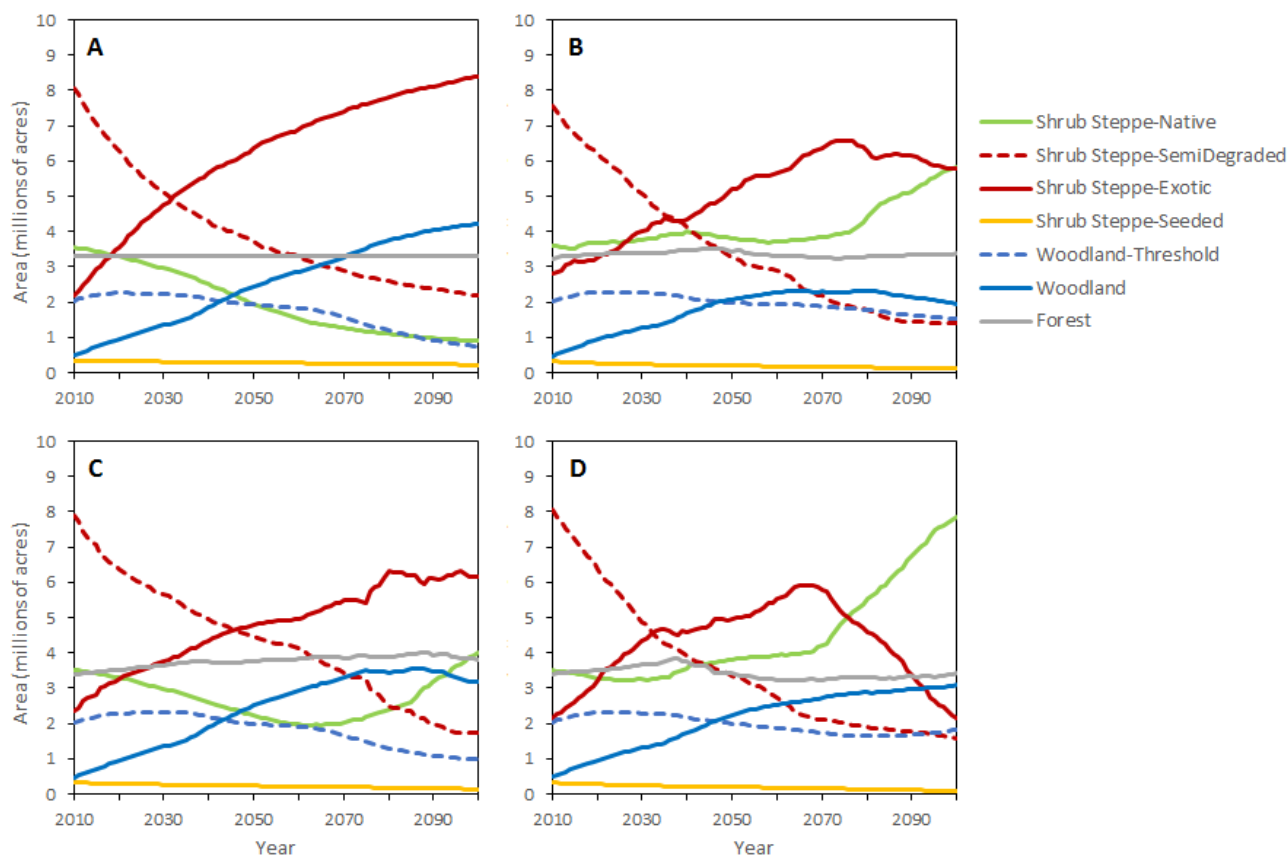


Figure 5. Shifts in vegetation composition (groups of state classes within the cSTSM) over time under continuing current climate (A), and the HadGEM (B), MRI (C), and NorESM (D) climate change scenarios. Projections are shown without active management (no management scenario).

3.2. Management scenarios

Management activities varied in their capacity to maintain desired vegetation composition. Treatments to control exotic grass were mostly ineffective in reducing the amount of exotic grass on the landscape (Figure 6A), and levels of exotic grass under current and restoration management scenarios were only slightly lower than under no management. Juniper treatments, in contrast, slowed woodland expansion substantially compared to no management. Current management treatments reduced juniper by an average of 850,000 acres by the end of the century compared to no management (Figure 6B). Restoration management reduced juniper woodlands by 1.6 million acres. However, across the entire landscape, juniper still increased over time under all climate-management scenarios.

Because we only modeled management treatments in priority treatment areas, which encompass half of the landscape, we also examined the effects of management within priority treatment areas only. In priority treatment areas, current levels of management were not sufficient to maintain juniper woodlands at current levels. However, the restoration management scenario was successful in maintaining juniper at similar to current levels under at least some climate scenarios (Figure 7).

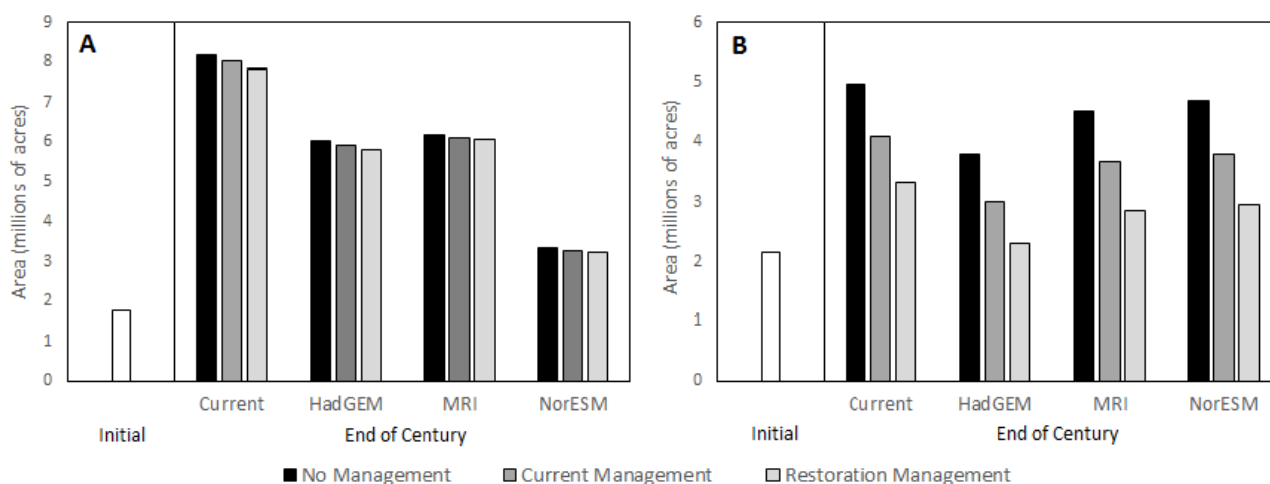


Figure 6. Projections of exotic grass (A) and juniper (phase I, II and III woodlands) (B) under four climate scenarios and three management scenarios. Results are summarized across the entire eastern Oregon study area. The left panel in each graph shows the initial mapped landscape conditions and the middle-right panels show projected average future conditions at the end of the century (2081–2100).

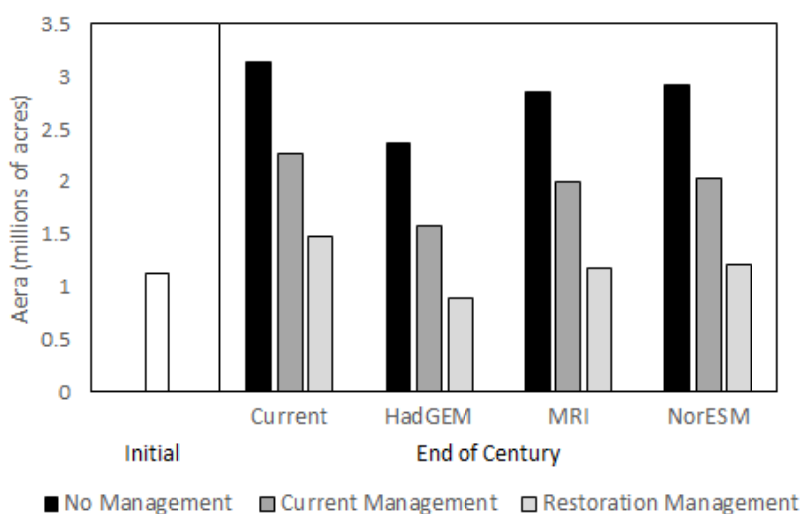


Figure 7. Projections of juniper (phase I, II and III woodlands) under four climate scenarios and three management scenarios. Results are shown for priority habitat areas only. The left panel shows the initial mapped landscape conditions and the middle-right panels show projected future conditions averaged for the time period 2081–2100. Exotic grass results are not shown, as they do not show different patterns from Figure 6.

3.3. Sage-grouse habitat

High-quality sage-grouse habitat, including only the state classes with the highest probability of species presence, occupied 4 million acres at the beginning of the simulation (Figure 8). General

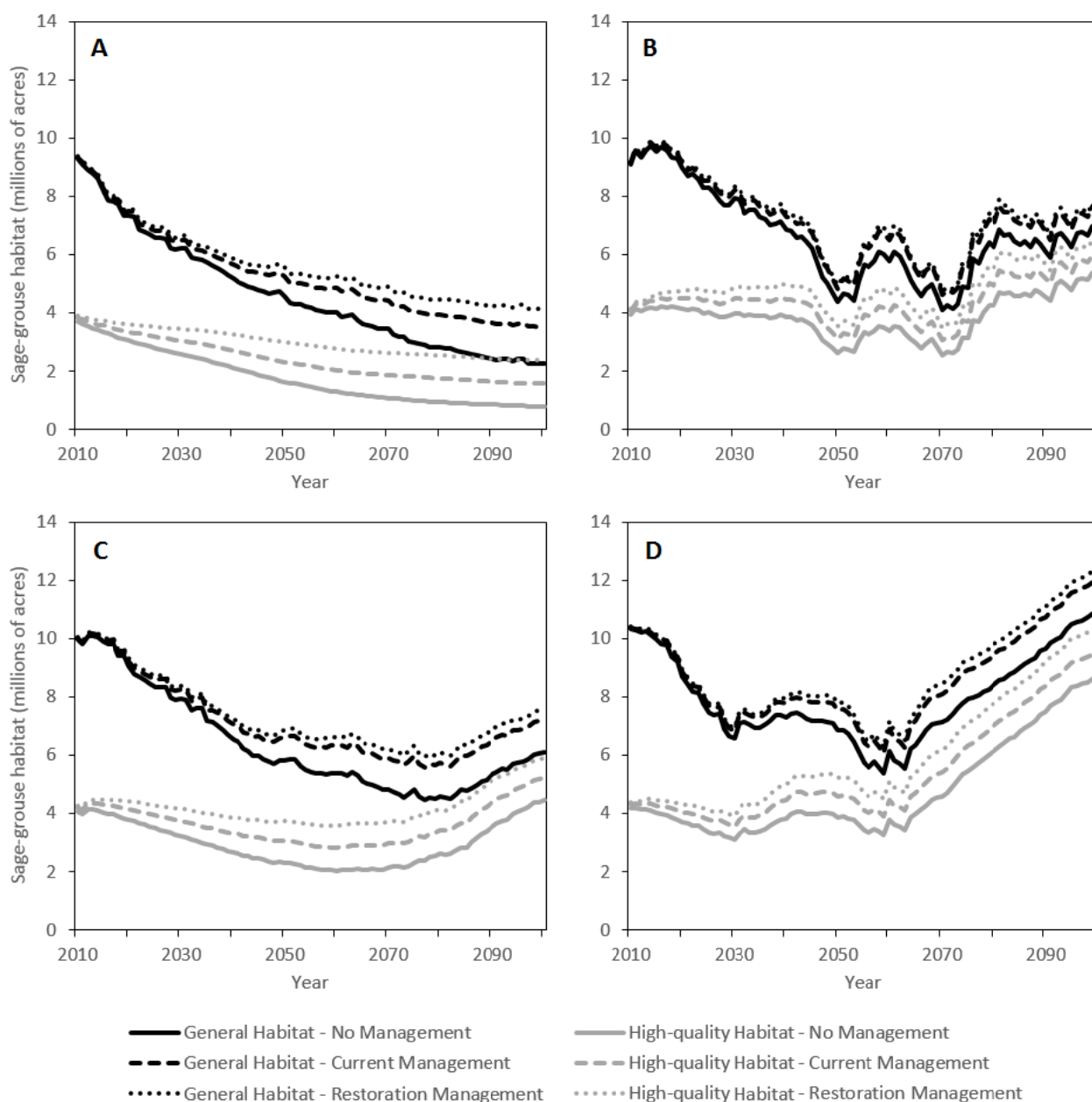


Figure 8. Projections of general and high-quality sage-grouse habitat under current climate (A), and HadGEM (B), MRI (C), and NorESM (D) climate change scenarios. General habitat is shown in black and high-quality habitat is shown in gray, and line type depicts each of three management scenarios. Results are summarized across the entire eastern Oregon study area.

habitat, including high-quality habitat as well as other less desirable state classes, such as some semi-degraded shrub steppe and phase I juniper woodlands, was mapped across 9.5 million acres at the initiation of the simulations. Projections of general sage-grouse habitat declined across all scenarios for the first few decades of the simulations, then diverged substantially among climate scenarios. Under current climate, high-quality sage-grouse habitat declined, but under the three climate change scenarios, projected high-quality habitat increased mid- and late-century, reaching

higher levels than currently mapped. The NorESM scenario showed the greatest increase in high-quality habitat, reaching double the mapped levels. Under current climate, general sage-grouse habitat declined to less than half of its current extent. However, under the three climate change scenarios, general habitat loss slowed mid-century and reversed in the last few decades of the simulation, particularly in the NorESM scenario, where general habitat increased to slightly above current levels. Management actions reduced losses of sage-grouse habitat in all climate scenarios. Under the current management scenario, projected end of century high-quality habitat increased by 590,000–870,000 acres and general habitat increased by 600,000–1.3 million acres, compared to the no management scenario. The restoration management scenario yielded even greater gains at the end of the century, with 1.1–1.7 million more acres of high-quality habitat and 740,000–1.9 million more acres general habitat than the no management scenario.

4. Discussion

Managing habitat for the greater sage-grouse presents many challenges, particularly as rangeland ecosystems face novel climatic conditions. Projections that integrate the many processes that threaten sage-grouse habitat—wildfire, invasive species, climatic shifts, and their interactions—and the management activities that are used to counter these threats provide essential information for planning effective management strategies for long-term habitat conservation. Our projections are intended to help understand vegetation trends over large spatial scales and long time frames and compare outcomes across a variety of potential future scenarios. We do not track many of the fine-scale habitat features that affect sage-grouse, nor do we model population dynamics, but instead focus on broader trends in potentially suitable habitat and other indicators of rangeland condition over the course of the century.

4.1. Potential vegetation types

Projected PVT extent diverges substantially from current climate under the three climate change scenarios. Dry and moist shrub steppe are the only PVTs modeled in this study that provide suitable habitat for sage-grouse, as they contain substantial components of sagebrush species and palatable forbs required for sage-grouse [6,9,48]. These two PVTs are also very different; the dry shrub steppe PVT is highly susceptible to exotic grass encroachment but is too dry for juniper, whereas the moist shrub steppe PVT has low susceptibility to exotic grass invasion but high probabilities of encroachment by juniper. Although dry shrub steppe dominated the initial landscape, moist shrub steppe increased and surpassed the extent of dry shrub steppe in all three climate change scenarios. This was due to a combination of increases in total annual precipitation and increased wildfire (discussed in Wildfire section, below) under climate change projections. Even in the HadGEM climate change scenario, which projected roughly equal precipitation to current levels in the period 2081–2100, there were periods of substantial gains in precipitation throughout the simulation. A total annual precipitation threshold was chosen to distinguish dry and moist shrub steppe vegetation types because it approximated the current distribution of dry and moist PVTs relatively well across the landscape, and precipitation is known to be one of the most important variables in structuring rangeland vegetation communities [6,49,50,51]. However, it is also known that the timing of precipitation events is important [52,53], and increasing temperatures will also undoubtedly affect

shrub steppe communities [53,54]. Our rule set for distinguishing between these two shrub steppe community types is simple, which is consistent with the type of generalized rule sets used in a model of global vegetation (see Supplementary MC2 Biogeography Model Description). It is important to note that our PVTs depict generalized vegetation types that are not species-specific. Sage-grouse are closely tied to sagebrush (*Artemisia*) species [7], and other shrub species such as antelope bitterbrush may provide similar structural habitat without the forage quality for sage-grouse.

Although they may be counterintuitive, our projections of increasing moist shrub steppe and declining dry shrub steppe are consistent with other, similar studies in the Pacific Northwest. In one recently completed study using MC2, moist shrub/woodland vegetation types increased substantially in the study region across multiple climate scenarios (Sheehan et al, manuscript in preparation). The Sheehan et al. study used a default rule set for the continental United States based on a carbon density threshold to separate the vegetation types we are considering to be dry and moist shrub steppe, with carbon accumulation simulated mechanistically by the biogeochemistry module of MC2 [55]. In fact, in this study, the dry shrub vegetation type was eliminated almost entirely in southeastern Oregon by the end of the century, as (primarily) moist shrub/woodlands and (in some climate models) C4 shrublands increased in area. In another study using the MC1 DGVM, Rogers et al. [56] projected declines in current shrubland vegetation and increases in woodland and forested types in the Columbia Plateau and south-central Oregon. Another study using the Lund-Postdam-Jena DGVM in the Pacific Northwest indicated that four out of five climate scenarios resulted in increasing woodland and forest cover in rangelands of the northern Great Basin and Columbia Plateau [57]. In these studies, vegetation shifts were largely due to increasing precipitation and warmer temperatures lengthening the growing season and allowing more carbon to accumulate in the ecosystem. Each of these studies organized ecological communities quite differently from ours, but they provide qualitative support for our projected declines in dry shrub steppe and increase in more productive, moist shrub steppe that is susceptible to tree encroachment.

Projections of xeric shrub steppe, distinguished by hot and dry summer conditions which are unfavorable for sage-grouse, were highly variable among climate scenarios. The projected extent of xeric shrub steppe varied from nearly zero in the wettest scenario (NorESM) to 27% of the landscape in the driest scenario (HadGEM) by the end of the century. This variability among climate models highlights the high level of uncertainty in future summer conditions, which are particularly critical for sage-grouse populations. A range-wide assessment of sage-grouse populations also suggests that drought conditions limit the distribution of sage-grouse, among other factors [58]. Projections of xeric shrub steppe were also highly variable from year to year, as they reflect interannual variability in summer temperature and precipitation. In the cSTSM, transitions between xeric shrub steppe and dry or moist shrub steppe were allowed to occur during any year without restriction, depending on the climate conditions in that given year. In contrast, shifts between other PVTs (e.g., forest to shrub steppe or dry shrub steppe to moist shrub steppe) were only allowed to occur from early-successional state classes, limiting these PVT shifts so they could only take place following a stand-replacing disturbance. Therefore, we see much more variability in xeric shrub steppe. It is also important to note that this xeric vegetation type may not be climatically unfavorable for sage-grouse in all seasons, and may provide important areas of connectivity between more favorable sites or provide habitat in cooler months. The summer drought-related threat to sage-grouse habitat cannot be managed per se, but information about where and how much summer droughts are likely to constrain sage-grouse habitat could help identify other priority areas for investing in active management to restore habitat.

Currently, estimates of summer droughts contain high uncertainty among climate models, but as models improve, the value of this information will increase for priority setting.

Although the extent of shrub steppe PVTs show marked changes over the length of the simulation, there is very little change in the extent of forests in the southeastern Oregon landscape. Conversion from shrub steppe to forested vegetation types in the MC2 model is defined by a carbon density threshold which is rarely crossed in the simulations, and under the relatively infrequent disturbance regime in the forested regions of the study area there is little opportunity to transition from forest to shrub steppe vegetation types. Under a warmer and wetter climate, however, fire-resistant pine species, such as Ponderosa pine, may increase in abundance and expand into shrub steppe along with or instead of juniper. Pine woodland dynamics are very different from juniper woodlands because many pine species are fire tolerant, whereas juniper trees are highly susceptible to fire-related mortality [59]. However, we could not capture this potential shift in species-specific vegetation dynamics using our methods. It also may take long periods of time for woodlands to establish under relatively warm and dry conditions across most of the study area, and we may not expect a complete shift in vegetation type within the 90 year time frame of the simulations.

There were no major novel vegetation types introduced into the study area under climate change in our MC2 simulations, although small areas of C4 (warm-season) grasslands and semi-desert shrublands (without a significant grass component) were present at low levels in some years. These vegetation types were combined with other similar vegetation types, as they occupied less than 2% of the initial landscape and never exceeded 5% of the landscape in any future year. Salt desert shrublands were modeled differently than in previous similar work [26], reflecting changes in the MC2 biogeography rule sets to better reflect our understanding of rangeland vegetation. In this analysis, salt desert shrublands were removed from the analysis or combined with dry shrub steppe (see Methods), and the xeric shrub steppe vegetation type was modeled instead to depict areas with a hot, dry summer climate.

4.2. Wildfire

In recent years, wildfires have burned large swaths of rangelands in eastern Oregon. Our results, along with several other studies [20,26,56,60], suggest that extreme fire years are likely to become more common in the region as climate changes and exotic grasses increase in abundance. Our wildfire projections indicate an average of 1 million or more acres per year burned in wildfire under the HadGEM and MRI climate change scenarios (Figure 4) at the end of the century, with many individual years likely to surpass the 1.6 million acres of burned area experienced in 2012. Increasing wildfire in all climate scenarios was driven in part by increases in exotic annual grasses, which tend to have a higher fire frequency due to accumulation of fine fuels [15,61]. However, exotic grasses exert a relatively minor effect relative to the changes in fuel buildup and moisture simulated in MC2 that are related to climate change, which caused a 2× to 4× increase in wildfire compared to current levels. Wildfire can have both positive and negative effects; wildfire is an important part of the natural shrub steppe vegetation dynamics and can aid in controlling juniper expansion, but it can also promote exotic grass invasion and remove the shrubs that are an essential component of sage-grouse nesting and brooding habitat [6]. However, open shrub steppe and herblands serve an important seasonal function as lekking grounds for sage-grouse, and sage-grouse will use recently disturbed sites to establish new leks [62]. Thus, patches of wildfire can ensure

presence of lekking grounds in the landscape by opening up shrub cover (and burning juniper woodlands), but its immediate effect is to reduce nesting and brooding habitat. Because our definition of habitat includes open areas associated with lekking, we show increases in sage-grouse habitat through time. However, other vegetation structures important to nesting and brooding may become limiting as post-fire herblands increase, and large or repeated wildfires may cause a longer-term loss of shrubs due to sagebrush dispersal limitations [63]. Summaries of our projections that exclude herblands from general and high-quality habitat show declines in sage-grouse habitat over time under all climate scenarios (data not shown). The prevalence of wildfire on the landscape may also influence the spatial relationship of different functional habitats, and sage-grouse nesting success is related to the spatial proximity of nesting habitat to leks [64].

Wildfire frequency is also an important component of our model projections, as most inter-PVT transitions (except those to/from xeric shrub steppe) are dependent on disturbances and are only allowed to occur from early successional state classes. Therefore, where projections include more wildfire, there will be more opportunities for climate change-related vegetation shifts. This has important implications for our results because the dry and moist shrub steppe STSMs incorporate very different wildfire dynamics. Dry shrub steppe has high susceptibility to exotic grass invasion, and invaded (both semi-degraded and exotic-dominated) state classes have higher wildfire probabilities than native shrub steppe, based on fire rotations derived from MTBS wildfire monitoring data [26,43]. In contrast, moist shrub steppe has greater resilience to exotic grass and can naturally recover from invasion, returning to native state classes with a lower fire probability. Therefore, because dry shrub steppe has more wildfire due to exotic invasion, there are more opportunities for transitions from dry to moist shrub steppe than vice versa. In combination with increases in projected precipitation, this contributes to the pattern of increasing moist shrub steppe on the landscape.

4.3. *Vegetation composition*

To examine patterns in more detailed vegetation composition and structure we can examine the extent of state class groups within the cSTSM. Model projections indicate a rapid increase in exotic grasses early in the century across all scenarios due to the large proportion (38%) of the landscape initially mapped in semi-degraded condition. In state classes that contain primarily native species, most disturbances such as wildfire and drought alone retain native species composition, but the interaction of excessive livestock grazing with drought or wildfire (post-disturbance grazing) can result in exotic grass invasion. However, once the state class has transitioned to semi-degraded shrub steppe, with partial dominance by both native and exotic grasses, the probability of transitioning to exotic grass-dominated state classes increases, and further degradation can be caused by individual disturbances. The large swaths of semi-degraded shrub steppe present in the initial landscape converted rapidly to exotic grass-dominated state classes in our simulations through wildfire (primarily) and grazing-related degradation following wildfire or drought. Once shrub steppe transitions to an exotic-dominated system, the area becomes even more unfavorable for sage-grouse because the increased wildfire frequency tends to remove shrubs and palatable forbs from the system.

Although exotic grass increased under all scenarios, projections under the three climate change scenarios contained lower levels of exotic grass compared to current climate. This is due to the

conversion of dry to moist shrub steppe PVTs, discussed previously. Because the moist shrub steppe STSM contains higher resilience to exotic grass invasion, the herbaceous layer recovers from exotic to native species in a relatively short time frame once it transitions to the moist shrub steppe PVT. This pattern is most dramatic in the NorESM scenario, where large projected increases in precipitation late in the century cause a rapid decline in both dry shrub steppe and exotic grass as the system shifts to moist shrub steppe. This pattern is counter to much of the literature, as many studies indicate that exotic grasses are likely to become an increasing problem under climate change [20,26,65,66,67]. However, some modeling suggests that certain currently invaded areas may be less favorable for exotic grasses under future climatic conditions [53,68]. For instance, Bradley [53] assessed several climate change scenarios across the western U.S. and found that most scenarios projected a decrease in climatically-suitable habitat for cheatgrass, although the median change scenario caused a slight increase. Bradley's work found precipitation timing and winter temperatures to be important in predicting climatic suitability for cheatgrass, and also highlighted the uncertainty in future climatic conditions, which may result in expansion, contraction or range shifts of the species. It is important to remember that our projections of exotic grass are closely related to the trends in the dry shrub steppe PVT using our modeling method, even though we know that their future distribution is unlikely to follow as closely as suggested in our results. Future work could incorporate additional information, such as a climatic suitability model for particular exotic species, which would provide additional information that could help determine where and if exotic grasses are likely to persist under climate change [53,68]. It is also important to consider the possibility that other exotic species currently absent or rare in the area may become a greater threat, such as red brome (*Bromus rubens* L.) or North Africa grass (*Ventenata dubia* (Leers) Coss.).

Juniper also expanded across the southeastern Oregon landscape without management treatments. Juniper trees provide perching sites for predators, and sage-grouse tend to avoid areas that have been encroached by juniper trees, even at relatively low cover [69]. Although juniper woodlands (phases II and III) occupied a small proportion of the initial landscape, the larger proportion of threshold woodlands (phase I) rapidly converted to woodlands under all climate scenarios. In the cSTSM, juniper woodlands are only modeled in the moist shrub steppe PVT, under the assumption that dry shrub steppe has insufficient moisture to support trees. Therefore, the potential extent of juniper is closely related to the extent of the moist shrub steppe PVT. Projections of juniper woodlands are also strongly affected by the wildfire frequency, as juniper trees are intolerant of fire and wildfire will cause a transition from juniper woodlands to shrub steppe state classes. Under current climate, the extent of the moist shrub steppe PVT remained a smaller proportion of the landscape, but most of the area within that PVT converted to woodlands. Under all three climate change scenarios, the extent of moist shrub steppe increased by two to three times its initial extent, but less of that was occupied by woodland state classes due to increasing wildfire. Therefore climate change had two opposing effects on juniper encroachment: it increased the area that is climatically suitable, but it also reduced juniper woodlands because they were being removed in wildfires. Our models do not take into account distance from juniper seed source, which may become more limiting under a future with more wildfire. It is also possible that some areas in southeastern Oregon will become susceptible to both juniper and exotic grass encroachment, which is currently uncommon.

4.4. Management scenarios

STSMs have been used in many applications to compare outcomes among multiple management scenarios and inform land management across broad spatial scales [39,40,42]. We modeled management across ownership boundaries and management allocations to assess the landscape-level effects of these scenarios. This approach can be particularly useful for managing “landscape species” such as sage-grouse, which requires large expanses of habitat with a variety of features [7,8] across large landscapes, including both public and private lands. The management scenarios considered in this study were developed to compare no actions, current practices, and a more intensive restoration scenario designed to improve sage-grouse habitat. We worked extensively with land managers to develop the scenarios, particularly to accurately represent current management treatment levels. Our model projections indicated that management treatments were generally effective in controlling juniper encroachment, although they needed to be implemented at higher than current levels to constrain juniper encroachment at or below current levels. In contrast, post-fire rehabilitation of exotic grass infestations was largely unsuccessful in dry environments where exotic species are most problematic.

Under the current management scenario, juniper treatments were primarily implemented on private and federal lands. Juniper treatments on private lands were quite extensive, with over 38,000 acres treated per year out of 4.4 million acres of private land in the study area. On BLM lands, roughly 30,500 acres of juniper were treated across all districts out of 14.5 million acres, a much smaller proportion. Many of these areas are too dry to support woodland encroachment, but on BLM lands that are susceptible to juniper encroachment an increased focus on juniper removal, as in the restoration scenario, could result in improved condition. It is important to note that we only simulated juniper treatments in priority treatment areas, which encompass 50% of the landscape, and therefore juniper continued to expand across the other half of the landscape in our projections. In the restoration management scenario, many managers expressed interest in using prescribed broadcast burning to control juniper woodland expansion in moist shrub steppe due to the lower cost per acre. The practice is currently not widely used and is controversial because it decreases sage-grouse habitat quality in the short term by removing shrubs [7]. However, there are also calls to return some of the natural wildfire cycle in moist shrub steppe as part of a broader ecosystem restoration strategy to restore natural processes and combat juniper encroachment [70]. Increasing wildfire may be unavoidable due to the effects of climate change, which can aid in keeping juniper at bay but also can pose additional risks to sage-grouse habitat.

Management to reduce exotic grasses in dry environments can be very difficult and expensive, with low success rates and high variability with seasonal and interannual weather patterns [25,71,72]. Most of the exotic grass treatments in the current management scenario consisted of post-fire restoration in exotic-dominated areas of dry shrub steppe. These treatments are often ineffective [72] and therefore have a low probability of success in the STSMs, and also have a limited opportunity for treatment (within 2 years of wildfire). Therefore, increasing the acres of post-fire restoration is unlikely to control the spread of exotic species. However, we also simulated restoration treatments in semi-degraded areas, where both exotic and native grasses are present, which shows improved outcomes and a higher success rate [71]. In the restoration scenario, the acres allocated to this treatment were increased to an annual treatment rate of 5,672 acres per year, but even this increased level is not nearly sufficient to combat exotic grasses across the 7.6 million acres of semi-degraded

shrub steppe mapped in southeastern Oregon. New technologies may be available in the future to improve the success rates of restoration treatments in exotic grass infestations. For now, prevention efforts are likely to be more effective than restoration, including measures to decrease propagule pressure from nearby populations, improving the resistance and resilience of sites to invasion, and locating and eradicating small invasive populations before they spread to an unmanageable size [73].

The management scenarios presented in this paper represent our best attempt to characterize current management practices in the region and a realistic alternative to improve sage-grouse habitat. To determine current management practices, we accessed a wide list of contacts and attempted to obtain all relevant data, but there is some uncertainty in the numbers we provide here. For private, state, and USFWS lands, we were able to obtain records of treatments implemented in the recent past with fairly high confidence. In the case of BLM treatments, however, it was difficult to determine the total number of acres treated. The NFPORS database maintained by BLM contained most or all of the relevant treatments, but treatments that were implemented in multiple years were entered into the database multiple times. For instance, a treatment that included juniper cutting, piling, and burning at the same location over a three year window was entered in the database three times. In order to avoid over-counting these treatments, treatment identifier numbers and spatial information was used to aid in estimating the total area treated, but there is higher uncertainty in these numbers. Despite this, our estimates of current management impacts are likely to be more accurate than generalized treatment rates based on simple assumptions about the proportion of the landscape treated (e.g., treating a defined percentage of encroaching juniper per year), that are often used in planning.

4.5. Sage-grouse habitat

Projections of potential sage-grouse habitat incorporate two distinct elements: climatic conditions, where conditions are unfavorable due to hot and dry summer conditions; and vegetation condition, where sage-grouse may be limited by habitat structure or composition. It is challenging to link our state classes to habitat, as the model state classes are fairly generalized compared to the landscape heterogeneity and complex habitat requirements for different seasons and life stages [6,7,9]. For instance, although we model presence of exotic grasses in the herbaceous layer, we do not track detailed composition of the herb and forb community, which will largely determine forage quality within more favorable habitat [7,74]. Even if our STSMs could accommodate such detail, accurately mapping detailed herbaceous species composition with spatial precision over very large landscapes is extremely difficult, especially in arid ecosystems where the above-ground appearance of many forbs is tied to sporadic rainfall events. We also do not represent seasonally-specific estimates of sage-grouse habitat, but instead use sage-grouse presence data from all seasons for an overall estimate of habitat. Future refinements to this work could track the most important or sensitive seasons of habitat and weight them with greater importance when determining the habitat value across the landscape. We separate out high-quality sage-grouse habitat from general sage-grouse habitat to provide a range of what may be considered potential future habitat.

It is important to emphasize that our habitat projections are based solely on vegetation and climate, and we are inferring sage-grouse habitat from those two factors. We do not account for many important anthropogenic features of the landscape, such as roads, power lines or other infrastructure. Therefore, in some cases, occupied habitat will likely be lower than our projections of potential habitat. Conversely, other areas we have identified as unsuitable may provide a role in

connecting more favorable habitat patches and our estimates of habitat may be conservative. We used a simple rule set to distinguish climatically unsuitable habitat, which undoubtedly oversimplifies the relationship between sage-grouse presence and climate. We used sage-grouse presence data to inform our climate rule set and our assignment of state classes to high-quality and general habitat, but we do not model population dynamics, demographic processes, or seasonally-specific estimates of sage-grouse habitat. Although our work provides only a simplified estimate of sage-grouse habitat, we believe that it is useful for comparing trends that emerge from different climate and management scenarios.

4.6. Model uncertainty and limitations

Simulation modeling can be a very useful tool to formalize assumptions about vegetation change, explore potential future trends, and compare outcomes across a range of scenarios. However, despite its utility, there are many reasons it should be interpreted cautiously. It is important to emphasize that simulation models are not a forecasting tool, but are most useful for comparisons among alternative scenarios. Integrating multiple models and simultaneously accounting for succession, disturbance, management, and climate change provides powerful information, but also requires many simplifying assumptions, as in all modeling studies. In addition, climate change projections contain high uncertainty, including uncertainty about greenhouse gas emissions levels, effects of greenhouse gas forcing on global and local climate conditions, and the impacts of those climatic conditions on vegetation communities [75]. We chose three climate models that encompass a range of future climate conditions in eastern Oregon to bracket some of the uncertainty in future climate, but there is still a large range of climatic uncertainty. This study should be evaluated along with many other lines of evidence, including both field-based and modeling studies, to evaluate likely trends in rangeland condition and determine the most effective management options.

In addition to the general caveats of simulation modeling, our specific approach has several limitations. We link together three models because of their complementary strengths, but each model carries a unique set of uncertainties and errors, which can compound as more models are brought together. Linking multiple models also creates greater complexity and creates new opportunities for error. Using this approach, we simulated changes in PVTs and vegetation state classes, which were pre-defined based on current vegetation conditions. When incorporating climate change effects, we could not simulate shifts in species composition, although we know that climate change is likely to reorganize communities as species and populations respond individually to environmental conditions [76]. We were able to incorporate climate-related trends in wildfire into the models, but we could not simulate direct effects of climate change on the rates or trends in other important processes, such as exotic grass invasion or juniper encroachment. Instead we simulated changes in the extent of rangeland PVTs and assumed that the probabilities of juniper encroachment, exotic grass invasion, succession rates, and other processes (excepting wildfire) within each PVT will remain similar under climate change. To our knowledge, there are currently no mechanistic, species-specific models for evaluating climate and management in shrub and grass communities across broad spatial scales. However, future work could integrate information about the expected effects of climate change on rates of species invasions and other important processes. For instance, exotic grass projections [53] could potentially inform our modeling process to produce more realistic results. Lastly, translating our vegetation model outputs to sage-grouse habitat is particularly tricky, since we are modeling relatively coarse categories of

vegetation and not accounting other factors besides climate and vegetation condition. However, the value of our study is the ability to bring together information about succession, disturbance, climate, habitat and management, and compare outcomes across a range of potential future conditions.

5. Conclusions

In this paper, we evaluate varying scenarios of future climate and management and their implications for rangeland condition and habitat quality. Resulting projections can help determine future climate-related risks, inform management across ownership boundaries, identify trends under current management practices, and evaluate alternative management approaches. Our simulations suggest that projected changes in climate may affect vegetation potential by increasing the amount of moist shrub steppe and causing periodic increases in xeric shrub steppe, where conditions are climatically unsuitable for sage-grouse. Wildfire frequency is likely to increase under all climate change projections. Rangeland condition is likely to decline in the future due to the prevalence of exotic grasses and juniper currently on the landscape, but projected future sage-grouse habitat varied among climate scenarios. Current levels of management treatments were not able to counter the threats of exotic grass and juniper encroachment in our simulations, but a restoration scenario with higher levels of treated juniper was effective in maintaining woodland encroachment near current levels in priority treatment areas. Projected impacts of climate change were more influential than management in eastern Oregon rangelands, although effects of climate change may be both positive and negative.

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Conflicts of Interest

All authors declare no conflicts of interest in this paper.

Supplementary

Online supplemental material: MC2 biogeography model description, and shrub steppe STSM state class descriptions and sage-grouse habitat values (provided as separate document).

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